African Journal of Agricultural Research Vol. 6(27), pp. 5905-5910, 19 November, 2011
Available online at http://www.academicjournals.org/AJAR
DOI: 10.5897/AJAR11.1192
ISSN 1991-637X ©2011 Academic Journals

Full Length Research Paper

Non-hydraulic root-sourced signaling and grain yield stability under shade of maize during progressive soil drying in soybean

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Accepted 20 October, 2011

Production practice shows shaded soybean in wheat-maize-soybean; relay strip intercropping system has better tolerance to drought as compared with sole cropping soybean. Our researches are to understand the reasons through non-hydraulic root signals (nHRS), yield and the relationships among them. Pot experiments were conducted with two soybean cultivars, under shade of maize (LI) and normal irradiance (HI). nHRS were traced during manipulative progressive soil drying period at branching stage under good soil conditions (HW), water stress treatment (LW), in 2010. Well-watered (WW), light drought (LD), moderate drought (MD) and severe drought (SD) were applied in 2009. In response to soil drying, nHRS appeared earlier in Gongxuan No.1 (GX) than Gongqiudou 05-8 (GQ) under two irradiance treatments, but it disappeared earlier for GX than GQ under normal irradiance. GX exhibited a wider average soil water content threshold range (TR) of nHRS under low irradiance. Drought stress significantly decreased the shoot dry mass, root mass and grain yield (P<0.05), excluding LD and nHRS treatments. Water use efficiency was significantly higher (P<0.05) in GX than GQ under drought conditions in both irradiances. In a conclusion, soybean cultivar GX has wider TR in low irradiance condition, light drought had no significant effect on yield, nHRS maybe beneficial to maintain soybean yield under drought condition.

Key words: Soybean, drought, shade, non-hydraulic root-sourced signal, water use efficiency, yield stability.

INTRODUCTION

As a result of population increase, the demand of food is ever increasing (Godfray et al., 2010). It is particularly important to increase the multiple crop index of land for the development of grain production. As the benefits of intercropping facilitation, yield advantage, high utilization efficiency of light and water, pest and disease suppression, and biological nitrogen fixation, legume/non-legume intercropping system using in the world widely (Bulson et al., 1997; Ghanbari et al., 2010; Hauggaard-Nielsen et al., 2001; Unkovich et al., 1997; Zhu et al., 2000). In China, half of the total grain yield is produced with multiple cropping, wheat/corn/soybean relay strip intercropping system is popular in South China (Yan et al., 2010). Plants usually expose to several stresses simultaneously under field conditions, limit of light and water availability are main environmental factors affecting relay strip intercropping soybean. The stresses may cause a variety of plant responses which can be additive, synergistic or antagonistic. The functional response to the combination of shade and drought involves biochemical, physiological, and structural changes at the leaf and whole-plant level (Aranda et al., 2005; Holmgren, 2000; Sack, 2004; Sack and Grubb, 2002). When the root system of a plant is subjected to water stress, the control of stomatal conductance (Gs) is the primary mean by

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Table 1. Soil water content (% of FWC) at the beginning, middle and end of the experiment (mean ± SE) in a subsample of pots under two light and two water levels combinations.

Time (days)	Low water		High water	
	HI	LI	HI	LI
0	80±0.8	80±1.2	79±1.4	80±0.8
10	51.8±0.7	53.7±1.1	76±0.9	78±1.1
20	25.5±0.6	29.8±0.2	79±0.8	81±1.1

HI represents normal irradiance; LI represents low irradiance, under the shade of light screen or corn.

which plants regulate water flow (Saliendra et al., 1995).

Decreasing Gs may or may not be associated with decreased leaf water potential (ψL), depending on the presence of either a non-hydraulic (chemical) root signal (nHRS) or of a hydraulic root signal (HRS) (Comstock, 2002; Min et al., 2000; Yao et al., 2001). The presence of nHRS and HRS is analyzed by the Gs and ψL responses of well-watered and water-stressed plants suggest the use of nHRS and HRS responses to decreasing soil water content (SWC) to evaluate plant-species drought tolerance (Croker et al., 1998; Mencuccini et al., 2000; Min et al., 2000; Xiong et al., 2006; Xu et al., 2006). Our objectives were to (1) determine the SWC at which nHRS and HRS occurred in the two cultivars under two light conditions during soil drying; (2) characterize yield stability responses of the two irradiance conditions under water stress conditions. These characterizations would make better understanding of the drought tolerance under low irradiance in the South of China.

MATERIALS AND METHODS

Plant material and growth conditions

Soybean cultivar Gongxuan No.1 (GX), a major component of South-western soybean cultivars, was tested in the experiments in 2009 and 2010; Gongqiudou 05-8 (GQ) was tested in 2010. Each seed was weighted individually and sown (in May 2009 /2010) in cylindrical pots of 14-L volume (23 cm high ×28 cm diameter), which contained 13 kg soil with 50% sand, 47.5% clay, 2.5% organic matter. The mixed soil was with fertilizer consisting of N=0.355 g, P_2O_5 =0.556 g and K_2O = 0.406 g. Fertilizers were applied after emergence, with 3 g Single Super Phosphate, 1 g Potassium Sulfate, and 1.5 g Urea per pot. The experiment was carried out in a glasshouse of the Sichuan Agricultural University (29°59' N, 103°00' E; at an altitude of 500 m) with an automatic closure system of upper ceiling when it was rainy. Soybean were subjected to two light levels:(1) high irradiance treatment (HI), receiving normal radiation from sun when it was sunny, and receiving available radiation inside the glasshouse when it was rainy (2009, 2010); (2) low-irradiance treatment (LI), covered by a light screen (65% of available radiation, Yaan Nongzhi CO., China, 2009), and under the shade of corn (2010). The experimental light treatments simulated the field conditions in the relay strip intercropping system, distinguishing two types of microhabitat: sloe cropping soybean (HI), relay strip intercropping soybean (LI).

Pots were watered every two days during the first stage of the experiment. Once the soybean seedlings reached V_5 stage (at the end of July 2009/2010), two months after sowing, half of the pots stopped receiving any watering (low-water treatment, LW) while the other half was kept continuously moist (high water treatment, HW, 75±2% of the field water capacity, FWC) in 2010. In 2009, four water treatments were applied, 1/4 of the pots was kept continuously moist (WW, 75±2% of FWC), and so did the light drought (LD, 60±2% of FWC), moderate drought (MD, 45±2% of FWC), severe drought (SD, 30±2% of FWC). In 2010, Low-water treatment simulated a typical climate situation of seasonal drought in south-western China, as compared to a continuously moist one (HW). During the experiment, we measured soil moisture (in volumetric water content, VWC), measured along the first 20 cm depth (with a TRIME-PICO, German) daily, in a subsample of five pots under different light and water treatments. Pots under LW decrease their water content differently for the two light treatments (Table 1). The duration was similar to the drought period under field conditions referring to seasonal drought.

Leaf gas exchange parameters

The net photosynthesis rate (Pn), stomatal conductance (Gs) and transpiration (E) were measured with a Portable Photosynthesis System (Model LI-6400, LI-COR Inc., Lincoln NE). Water use efficiency (WUE) was calculated as Pn/E. The parameters were measured after water stress was applied, at 08:00 am to 12:00 am daily. Five plants were randomly chosen, and one of the most recently expanded leaves was selected from each plant, four replications. The PAR, provided by a LED light source, was set to 1200 μmol m^{-2} s^{-2}. The flow rate of air through the sample chamber was set at 500 $\mu mol^{-1} s^{-1}$, and the leaf temperature was maintained at 25±0.8°C by thermoelectric coolers. The CO_2 concentration of the chamber was adjusted to 400 μl l^{-1} with the system's CO_2 injector.

Relative water content

The relative water content (RWC) of leaf was calculated using the standard formula [(FW−DW)/ (HydW−DW)×100] previously determined by Farrant (2000), where FW, HydW and DW are the leaf fresh weight, hydrated (full turgor) and dry weights, respectively. Soybean leaves were harvested daily after water stress was applied, V_5 stage (at the end of July 2009/2010). The hydrated weight was determined by weighing the leaf after 24 h of immersion in distilled water in a sealed flask at room temperature. Dry weight was determined gravimetrically after drying to steady weight at 70°C in an oven. The nHRS was judged to begin when there was a significant lowering of leaf stomatal conductance without change in leaf RWC (compared with Gs in 75±2% FWC), and the HRS was judged to begin when there were significant

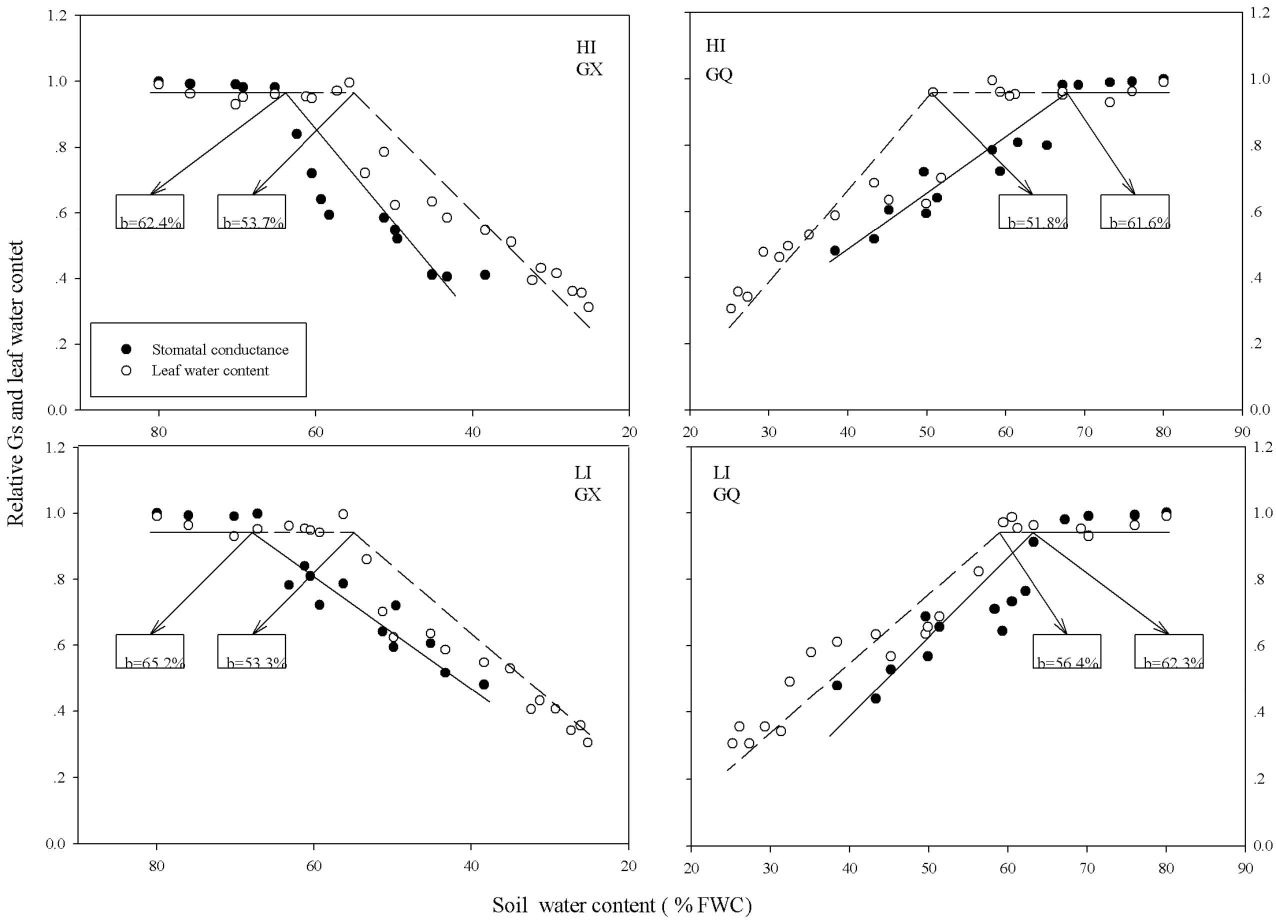

Figure 1. Relative stomatal conductance and leaf water content of Gongxuan No.1 (GX) and Gongqiudou 05-8 (GQ) cultivars in response to progressing soil drying at branching (V_5) stages. HI represents normal irradiance; LI represents low irradiance, under the shade of light screen or corn.

differences for both of the aforementioned leaf parameters.

Biomass allocation and yield measurement

Plant biomass was measured using 3 plants per pot at growth stage R_5 (initial seed fill), four replications. After separating plants into leaves, stems and roots, dry matter was determined after drying for 48 h at 70°C, and weighed them. Harvested all the plants in the pots, when 95% of pods became mature color (full maturity, R_8 Stage), each treatment had five replications.

Statistical analysis

The experiments were laid out as a factorial design, light irradiances were the main-plot factors, and soil water contents were the subplot factors. Results were analyzed by two-way analysis of variance (LSD) and means were compared by Duncan's multiple range tests at P<0.05, using the software Statistical Package for the Social Sciences (SPSS) version 11.5. The relationships of Gs and relative water content of leaf (RWC) to SWC were evaluated using a linear-plateau model. The relative values of Gs and RWC equal:

1 if Ci ≤SWC ≤ 1 (1a)

1-[A×SWC- Ci] if SWC≤ Ci (1b)

Where A is the slope of the linear Equation 1b and Ci is the threshold of SWC at which the measured traits started to diverge, that is, increase or decline from 1. Data were subjected to ANOVA procedures (SAS Inc., Cary, NC, USA) to estimate A and Ci in the linear-plateau model [Equation 1]; PROC NLIN of PC SAS was employed. Statistical separations between different plant physiologic processes were from comparisons of coefficients in Equation 1b at P<0.05 (Liu et al., 2002).

RESULTS

Threshold ranges of nHRS and HRS in soybean varieties

The Gs decreased when soil water content (SWC) fell below 65.2 and 62.3% for GX and GQ under low irradiance respectively, before leaf RWC began to decrease (Figure 1). With soil water depletion, leaf RWC decreased; when SWC was reduced to 53.3 and 56.4% for GX and GQ under low irradiance, respectively, leaf

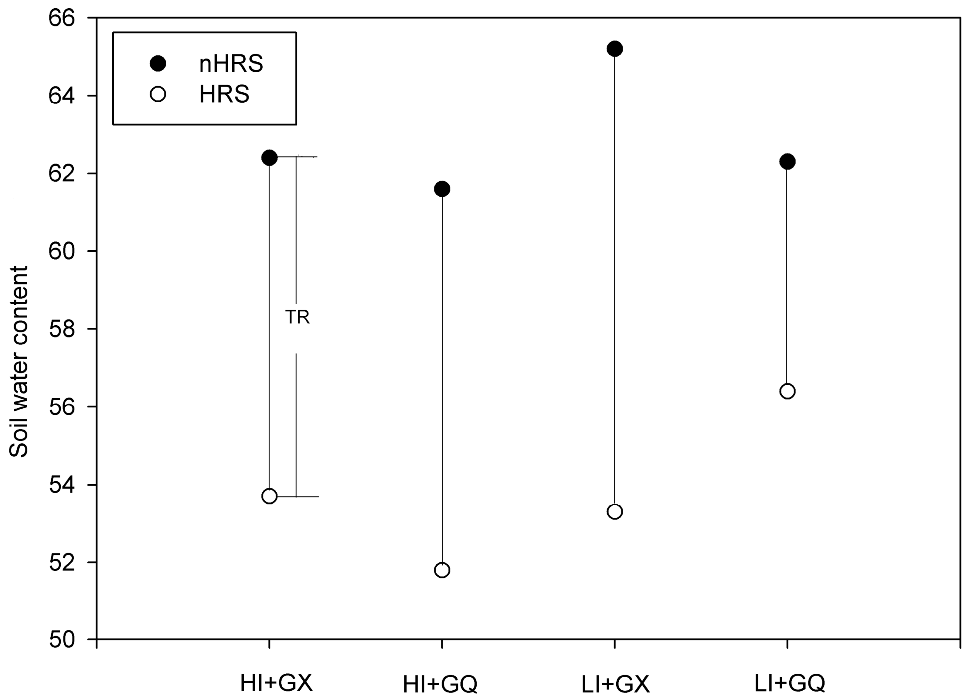

Figure 2. Soil water content (SWC, as % of FWC) thresholds for non-hydraulic root-sourced signal (nHRS) appearance and hydraulic root signal (HRS) appearance for Gongxuan No. 1(GX) and Gongqiu 05-8(GQ) cultivars at V_5 stage. Filled circle and open circles indicated the upper limit and the lower limits, respectively; TR represents ranges of soil water content thresholds of non-hydraulic root-sourced signaling. HI represents normal irradiance; LI represents low irradiance, under the shade of light screen or corn. Soil water content was represented as % of field water capacity (FWC).

RWC was significantly lower. The SWC thresholds of leaf Gs and RWC, relative to well-watered controls, were determined by linear-plateau functions (equation 1a and b). When SWC decreased below the thresholds, leaf Gs and RWC declined linearly. The SWC thresholds for Gs were 62.4 and 61.6% for GX and GQ under high irradiance and for leaf RWC they were 53.7 and 51.8% for GX and GQ under high irradiance, respectively.

The threshold range (TR) was the difference in threshold of SWCs between HRS and nHRS (that is, TR = the upper limit – the lower limit; the upper limit of the TR was threshold SWC of the nHRS, and the lower limit was threshold SWC of the HRS). GX cultivar under low irradiance had the widest soil moisture threshold range (53.3 to 65.2% FWC, that is, 11.9%); GQ cultivar under low irradiance had the narrowest range (56.4 to 62.3% FWC, that is, 5.9%); but GQ cultivar under high irradiance had wider range between 51.8 and 61.6% FWC (that is, 9.8%) as compared to TR under low irradiance (Figure 2).

Water consumption and water use efficiency

Whole season water consumption significantly decreased with the drought duration p rolonged; there were no significant differences among light and cultivar treatments (Table 2). WUE for GX was significantly higher than that of GQ under low irradiance. WUE under light drought (short duration of drought stress) did not reduce, it increased oppositely; WUE values under nHRS were the highest among all the soil moisture treatments.

Dry weight and grain yield

Root, stem, leaf dry weight and grain yield were significantly lower under drought conditions than those of controls, excluding light drought and nHRS treatments (Table 3). The data in 2009 showed that grain yield of GX under moderate stress was greater than those of severe drought, light drought and well- watered control treatments. Grain yield of GX by rewatering at commencement of RH was higher than other treatments in the experiment of 2010. Grain yield under low irradiance was lower than that of high irradiance, but the difference was not significant. Light drought reduced leaf dry weight, but did not decrease root and stem dry weight. Yield under light drought was greater than controls under two irradiance treatments; under low irradiance yield of moderate drought was greater than light drought even. nHRS was beneficial to maintain a higher plant biomass

Table 2. Whole season water consumption by rewatering at the commencement of nHRS, RH, HRS, TW (kg/pot) and water use efficiency (μmol $mmol^{-1}$).

Harvest time	Whole season water consumption(kg/pot)				Water use efficiency (μmol $mmol^{-1}$)			
	HI		LI		HI		LI	
	GX	GQ	GX	GQ	GX	GQ	GX	GQ
CK	57.7^{a}	57.9^{a}	51.1^{b}	51.3^{b}	4.074^{b}	4.304^{b}	3.731^{c}	2.208^{d}
nHRS	45^{c}	47.1^{bc}	45.2^{c}	47.3^{bc}	6.633^{a}	6.344^{a}	6.153^{a}	6.452^{a}
RH	28.7^{d}	29.7^{d}	28.8^{d}	29.9^{d}	3.402^{c}	1.982^{d}	6.468^{a}	3.962^{bc}
HRS	28^{d}	28.5^{d}	28.2^{d}	28.6^{d}	3.176^{c}	1.755^{de}	1.978^{d}	0.7521^{de}
TW	15.9^{e}	16.7^{e}	16.1^{e}	16.9^{e}	0.2317^{e}	0.194^{e}	0.5212^{e}	0.2312^{e}

HI represents normal irradiance; LI represents low irradiance, under the shade of light screen or corn. CK represents well watered controls; nHRS represents the outset of non-hydraulic root signals; HRS represents the outset of hydraulic root signals; RH exists between nHRS and HRS; TW represents temporary wilting. Within columns, means of the same character followed by the same small and capital letters are not significantly at the 0.05 and 0.01 levels of probability according to LSD test, respectively.

Table 3. Root dry weight (g pot^{-1}), stem dry weight (g pot^{-1}), leaf dry weight (g pot^{-1}), and grain yield (g pot^{-1}) for GX under high irradiance and low irradiance, in different water stress treatments.

Year	Irradiance	Water treatment	Root dry weight	Stem dry weight	Leaf dry weight	Grain yield
2009	HI	WW	7.56^{ab}	20.49^{a}	6.00^{a}	17.48^{ab}
		LD	8.97^{a}	17.76^{b}	5.28^{ab}	18.20^{a}
		MD	7.26^{ab}	12.45^{cd}	3.81^{bcd}	16.19^{bcd}
		SD	2.70^{d}	7.23^{e}	3.12^{cd}	15.52^{de}
	LI	WW	5.70^{bc}	13.65^{c}	4.83^{abc}	15.72^{cde}
		LD	6.93^{b}	16.14^{b}	4.23^{abc}	16.96^{abcd}
		MD	4.53^{cd}	10.74^{d}	3.21^{cd}	17.25^{abc}
		SD	3.03^{d}	3.60^{f}	2.22^{d}	14.59^{e}
2010	HI	CK	4.85^{bcd}	15.25^{b}	14.87^{b}	18.85^{a}
		nHRS	8.64^{a}	20.25^{a}	21.23^{a}	19.59^{a}
		RH	6.57^{ab}	13.99^{b}	12.26^{bc}	16.65^{ab}
		HRS	4.16^{bcd}	8.90^{c}	9.28^{cde}	14.55^{bcd}
		TW	3.30^{cd}	7.64^{c}	5.48^{ef}	14.09^{bcd}
	LI	CK	4.57^{bcd}	8.65^{c}	7.91^{de}	14.68^{bcd}
		nHRS	6.07^{abc}	13.52^{b}	12.57^{bc}	15.60^{abc}
		RH	5.36^{bcd}	14.40^{b}	12.52^{bc}	13.24^{bcd}
		HRS	5.43^{bcd}	13.11^{b}	10.56^{cd}	12.24^{cd}
		TW	2.56^{d}	8.60^{c}	3.82^{f}	10.51^{d}

HI represents normal irradiance; LI represents low irradiance, under the shade of light screen or corn. WW represents well water (75±2% of FWC), LD represents light drought (60±2% of FWC); MD represents moderate drought (45±2% of FWC); SD represents severe drought (30±2% of FWC). CK represents well watered controls; nHRS represents the outset of non-hydraulic root signals; HRS represents the outset of hydraulic root signals; RH exists between nHRS and HRS; TW represents temporary wilting. Within columns, means of the same character and same season followed by the same small and capital letters are not significantly at the 0.05 and 0.01 levels of probability according to LSD test, respectively.

and grain yield, rewatering at the commencement of nHRS obtained the highest root, stem, leaf biomass and the greatest yield.

DISCUSSION

Root sensing of water deficit refer to chemical signals transport through the xylem and ultimately reduce leaf transpiration and leaf growth. Chemical signals are differentiated from hydraulic signals (Gollan et al., 1986), but both are important to reduce stomatal conductance and leaf growth under conditions of water deficit.

Chemical signals most probably dominate during early stages of stress before hydraulic signals are produced

(Goodger et al., 2005). Research (Ali et al., 1999) showed that nHRS caused early drought adaptation at mild water stress by reducing leaf growth and Gs and the hastening of heading and flowering. Mingo indicated that fruit growth rates responded to changes in soil moisture status was not always regulated by hydraulic changes; nHRS regulated tomato fruit growth during soil drying (Mingo et al., 2003). Xiong indicated that FWCs in the non-hydraulic early warning response was a critical trait for plant adaptation to the drought conditions (Xiong et al., 2006). The start and closure of nHRS that reduces the aperture of stomata, as indicated by reduction in Gs values, began at different SWC according to cultivars (Xiong et al., 2006).

In this study, signaling in GQ was in the narrow range of about 61.6 to 51.8% under low irradiance, GX was in the wide range of about 62.4 to 53.7%. Different cultivars tended to have different threshold range, and the same cultivar had different threshold range under different light conditions. GX under low irradiance tended to have a wider threshold range as compared with the treatment of high irradiance. These results suggest that GX cultivar under low irradiance may have better non-hydraulic root-sourced signaling system, so that the water tension cue(s) from drying soil to trigger the non-hydraulic signal is sensed earlier and the signal is sensed longer, than in high irradiance treatment. Under soil drying, soybean respond to water deficit earlier is beneficial to the maintenance of plant water status through improved/ stabilized water uptake capacity at constant or decreesing transpiration. GQ cultivar may not be suitable to cultivate in relay strip intercropping system, with low irradiance available. Drought significantly affected soybean growth; low irradiance was efficient for soybean GX to response drought earlier. This result would provide breeders with a possible breeding direction to improve soybean yield under drought stress.

ACKNOWLEDGEMENTS

The research was supported by the National Program on Key Basic Research Project (2011CB100402), Public Research Funds Projects of Agriculture, Ministry of Agriculture of the Peoples Republic of China (201103001), Program on Industrial Technology System of National Soybean (CARS-04-PS19), and National Natural Science Foundation of China (31071373). The author Jing Zhang is a recipient of a scholarship from the China Scholarship Council.

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